

Emergence of hybridogenous polymorphism in the *Oenanthe picata* complex

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The simultaneous existence in a population of 2 or more discrete phenotypes ('morphs', 'phases', 'varieties') belonging to one sex and age-class (e.g. sexually mature males) is generally known as genetic polymorphism. Although polymorphism of this kind is by no means rare in birds, many questions concerning the causal relationships and biological significance of the phenomenon remain open. One such question concerns the mechanisms by which polymorphism originates within a population.

Alongside the prevailing view that polymorphism is caused by a process of mutation (i.e. spontaneous events taking place purely within a given population), the idea has also been expressed that it may have evolved on the basis of gene exchange between originally independent populations (see e.g. Haffer 1977: 41).

In this paper an attempt will be made to reconstruct the historical process which led to 'hybridogenous polymorphism' (see Panov 1989), and other types of variation resulting from hybridization, in Palaearctic wheatears of the *Oenanthe picata* complex. Until recently, geographical variation in this complex was generally treated as a variation in the relative numbers of 3 colour 'varieties' or 'morphs' (*picata*, *capistrata* and *opistholeuca*). The origin of this supposedly discrete variation was seen in terms of changes in the frequency of alleles of certain genes responsible for male plumage coloration (e.g. Mayr & Stresemann 1950, Paludan 1959, Loskot 1972, Stepanyan 1978).

Our hypothesis (Panov 1974, Panov 1989) is based on a completely different premise, namely that the 3 plumage types in the Eastern Pied Wheatear *O. picata* in fact characterize 3 originally independent taxa, each of which evolved in its autochthonous range in accordance with the principles of geographical speciation. The present distribution pattern of individuals with the 3 different plumage types (and also of various 'intermediate' phenotypes) is explained by the processes whereby the gene pools of the 3 original populations became intermixed.

We shall examine here the 3 main types of integration processes which correspond to the varying nature and intensity of gene flow between erstwhile independent population systems.

1. Limited hybridization in places where the breeding ranges of the original forms abut (parapatry) or overlap to an insignificant extent (allo-parapatry). The result may be the formation of a narrow zone of hybridization.

2. Prolonged existence of such a zone may lead to the establishment of gene flow from the zone of hybridization into the ranges of the parent forms. Gene migration takes place through the generations and also through dispersal by individuals of one form into the range of another and by birds of hybrid origin straying into the ranges of both forms.

3. Should hybridization become more firmly established, the hybrid zone may expand and a panmictic hybridogenous population with polymorphic features be created, which will eventually acquire a range of its own.

In the years 1966–1990, we studied the phenotypic composition of Eastern Pied Wheatear populations at 10 localities in the bird's Central Asian breeding range. A total of 279 males and 168 females was trapped, and 347 chicks were individually marked, 34 of these being retrapped in subsequent years. Twenty-eight chicks were reared in captivity until they had acquired adult plumage, and 296 specimens (217 males, 79 females) were examined in museum collections.

Divergence within the 'Eastern Pied Wheatear' complex

Plumage colour and sexual dimorphism

The 3 forms which constitute this complex were originally described as independent species under the names *Saxicola picata* Blyth, 1847, *S. opistholeuca* Strickland, 1849, and *S. capistrata* Gould, 1865. They are well differentiated in plumage coloration, not only of males but also females (Fig. 1) and, perhaps, also in juvenile plumage (Zarudnyi 1923).

Unlike the 2 others, the form *capistrata* shows clear sexual dimorphism, females being distinguished from males by the complete absence of melanins in their plumage. In the forms *picata* and *opistholeuca*, female plumage is variable, and females which are virtually indistinguishable from males are not uncommon (Panov 1989) (Fig. 2). There is some basis for the supposition that the contrasting male-type plumage is acquired by female *picata* and *opistholeuca* with age (Panov *et al.* in press).

Biometrics

In those parts of its range where it is not in contact with the other 2 forms, *picata* has a significantly shorter wing than populations from the autochthonous ranges of *capistrata* and *opistholeuca*. Maximum wing-length tends to be characteristic of populations from northern parts of the autochthonous range of *capistrata*, far from the ranges of the other 2 forms (Table 1; see also Panov *et al.* in press). Wing-length in this case is probably a reliable indicator of general body-size.

The weight of *picata* males from various localities in Turkmenistan ranges from 19.7 ± 0.2 g to 21.5 ± 0.4 g (mean of whole sample of 102 males 20.2 ± 0.2 g). Similar values are quoted by Desfayes & Praz (1978) for southern Iran. Our sample of *picata* males differs significantly ($t = 4.69$, $P < 0.001$) from a sample of 6 males from the autochthonous range of *capistrata* (23.3 ± 0.6 g). The latter value matches weight data for 10 *capistrata* males (23.5 ± 0.5 g) from northern Afghanistan (see Paludan 1959). Further data in Paludan (1959) indicate a mean weight of 21.7 ± 0.4 g for 8 *picata* males from western Afghanistan, and 22.1 ± 0.33 g for 10 *opistholeuca* males from the autochthonous range of that form; the differences between *capistrata* and *picata* are significant ($t = 3.1$, $P < 0.01$), also those between *capistrata* and *opistholeuca* ($t = 2.4$, $P < 0.05$); between *picata* and *opistholeuca* the differences are not significant ($t = 0.77$).

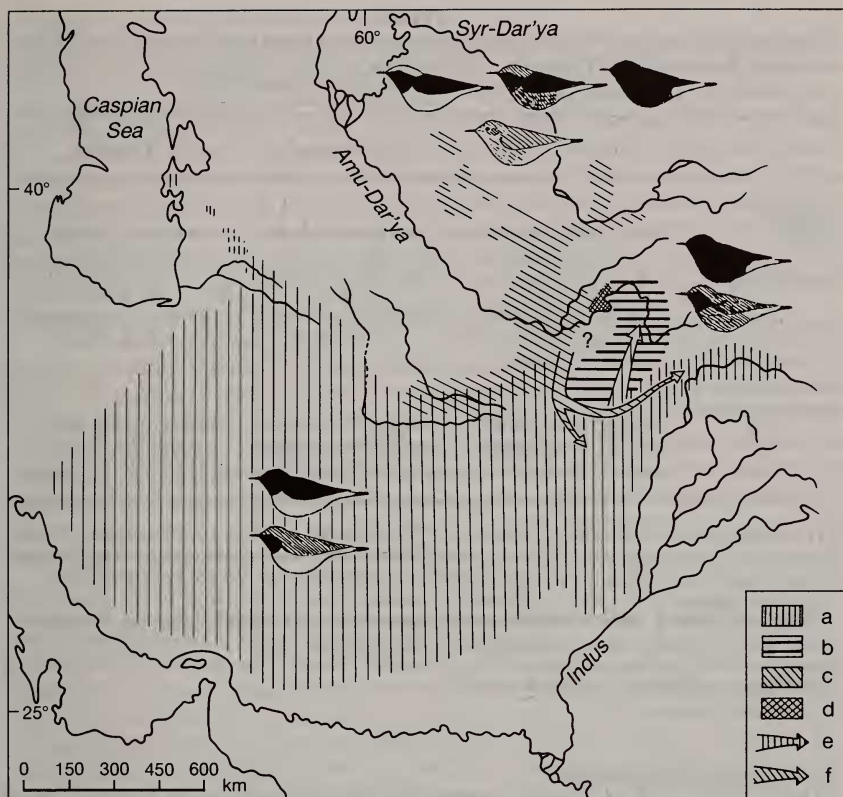


Figure 1. Ranges of the form (a) *picata* (b) *opistholeuca*, (c) polymorphic hybridogenous population '*capistrata* × *opistholeuca*' and (d) hybrid population '*capistrata* × *opistholeuca*' × *opistholeuca*. Main directions of dispersal by the form *picata* into the range of (e) *opistholeuca* and (f) by individuals of the *capistrata* phenotype into the range of *picata* are indicated by arrows.

Top row:	♂ <i>capistrata</i>	♂ <i>evreinowi</i> ♀ <i>evreinowi</i>	♂ <i>opistholeuca</i>
Middle row:			♂ <i>opistholeuca</i> ♀ <i>opistholeuca</i>
Bottom row:	♂ <i>picata</i> ♀ <i>picata</i>		

Decreasing body-size in the order *capistrata*—*opistholeuca*—*picata* is also reflected in the different egg dimensions.

Eggs of pairs with *capistrata* males are significantly larger (in width) than eggs from clutches of the form *picata* in its autochthonous range (16.0 ± 0.6 , $n=62$ and 15.5 ± 0.09 , $n=49$, respectively; $t=4.55$, $P<0.0002$). Eggs of the form *opistholeuca* occupy an intermediate position in this parameter (15.7 ± 0.10 mm, $n=35$).

TABLE 1

Means (mm) \pm standard deviation, sample size and range (mm) of wing-length (unflattened chord) of Eastern Pied Wheatears, the *Oenanthe picata* complex, from autochthonous ranges of the forms *picata*, *capistrata* and *opistholeuca*

	Males > 1 year	1st-year males	Females
Range of:			
<i>picata</i>	90.4 \pm 0.2 (n = 110) 84.0–95.3	88.0 \pm 0.2 (n = 81) 84.6–92.3	85.7 \pm 0.3 (n = 81) 75.9–89.9
<i>opistholeuca</i>	92.3 \pm 0.3 (n = 24) 88.2–95.3	90.3 \pm 0.5 (n = 10) 87.0–92.0	87.1 \pm 0.3 (n = 20) 85.1–89.9
<i>capistrata</i> *	92.9 \pm 0.3 (n = 61) 88.0–97.7	90.5 \pm 0.3 (n = 45) 86.3–94.4	87.1 \pm 0.3 (n = 38)** 83.0–92.6
Comparison by Student's <i>t</i> -test			
1:2	<i>t</i> = 5.28, <i>P</i> = 0.0001	<i>t</i> = 4.22, <i>P</i> = 0.0002	<i>t</i> = 3.41, <i>P</i> = 0.001
1:3	<i>t</i> = 8.10, <i>P</i> = 0.00001	<i>t</i> = 6.51, <i>P</i> = 0.00004	<i>t</i> = 2.97, <i>P</i> = 0.01
2:3	<i>t</i> = 1.53, <i>P</i> = 0.14 (n.s.)	<i>t</i> = 0.28, <i>P</i> = 0.78 (n.s.)	<i>t</i> = 0.07, <i>P</i> = 0.96 (n.s.)

*Hybridogenous polymorphic populations '*capistrata* \times *opistholeuca*'. Analysis of combined sample comprising the phenotypes *capistrata*, *opistholeuca* and *evreinowi* (differences between samples of these phenotypes within this population group are not significant).

**In this sample 24 females are from the southern part of the range of the populations investigated, where there is perhaps some influence from genes of the small form *picata*. Mean for 14 females from northern part of the range of '*capistrata* \times *opistholeuca*' populations is 88.6 \pm 0.5 mm (difference from mean of females from autochthonous range of *opistholeuca* significant, *t* = 2.49, *P* = 0.05).

Communication behaviour

We compared the vocalizations of the 3 forms of Eastern Pied Wheatears, the motor patterns of their communication behaviour and the organization of the main types of social interactions (Kostina & Panov 1981, Panov 1989). As a whole, the communication systems of these forms are structurally identical, though their component elements are subject to considerable variation. Because of this, data presented here on apparent quantitative differences between some homologous components are best regarded as provisional.

Of the 6 call- and 4 song-types characteristic of all 3 forms, differences were found in one call-type—in *picata* and *capistrata* (data for *opistholeuca* are insufficient for comparison)—and 2 song-types. Advertising song differs most conspicuously from the general type in the form *opistholeuca* in its autochthonous range.

The motor patterns of communication behaviour appear identical, apart from certain tendencies for variation in the frequency with which particular elements of the patterns are used by one or another of the 3 forms. Comparison of the organization of behaviour during pair-formation found *capistrata* females to be more aggressive than *picata* females. Pre-copulatory interactions are very similar in the forms *picata* and *opistholeuca*, but they differ from those of *capistrata*, whose behaviour in this context is closer to Finsch's Wheatear *O. finschii*.

Habitat and timing of breeding season

The form *capistrata* inhabits arid low hills and clearly avoids nearby high-mountain massifs. In the area of the former USSR, it ascends as a breeding bird to altitudes of c. 1500 m. The form *opistholeuca* is found up to 2000–2500 m in the Pamiro-Alay, with *picata* also ascending to that altitude from the south. In the mountains of southern Iran, *picata* breeds in the zone between 2100 and 2400 m, occasionally ascending to 2700 m (Desfayes & Praz 1978). Originally typical inhabitants of rocky mountain habitats, *picata* and *opistholeuca* are spreading into broken semi-desert terrain originally occupied by the form *capistrata*, with which they now hybridize. In these areas of secondary contact, individuals of all 3 phenotypes nest side by side in the same habitats.

The form *capistrata* is probably prevented from expanding into the high-mountain parts of the ranges occupied by the other 2 forms because of its characteristically early breeding season. Thus, the start of nest-building by *capistrata* has been recorded in southern Uzbekistan (c. 38°N) around 6–15 March, while at approximately the same latitude in Badkhyz (southeast Turkmenistan) *picata* does not begin nesting before 5–12 April. During this period in the range of *opistholeuca*, near where it abuts *capistrata*, arrival of females and pair-formation are not yet concluded (for details see Panov 1989).

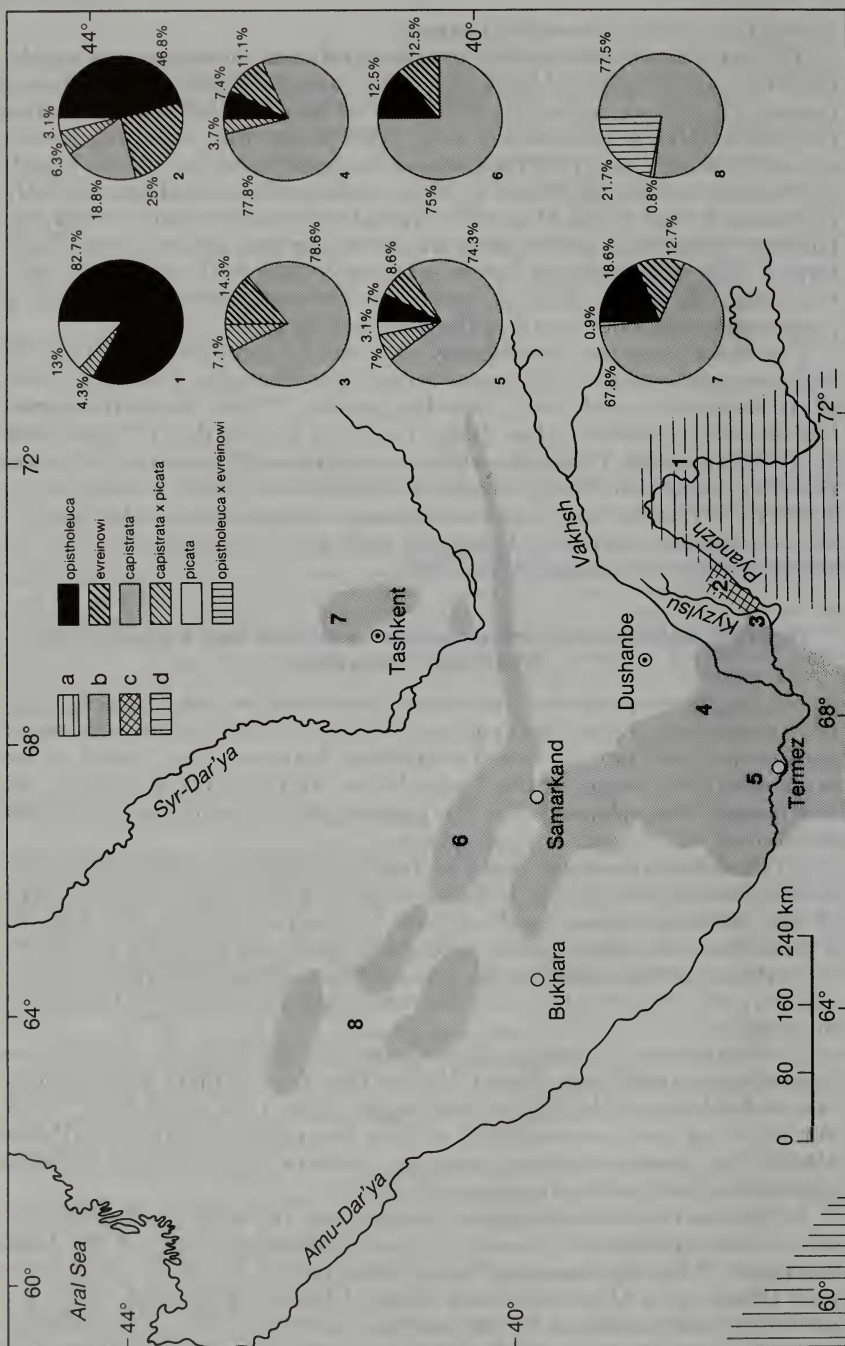
Hybridization and its consequences within the 'Eastern Pied Wheatear' complex

According to the proposed hypothesis, there exist within the complex at the present time 3 population groups with a relatively stable phenotypic appearance, and populations intermediate between them found in the areas where the ranges of the 3 population groups referred to above are contiguous, or overlap or both. The phenotypically stable populations are as follows:

1. Populations generally with the diagnostic features of the form *picata* (which has the largest area of distribution in western and southern parts of the range occupied by the whole *O. picata* complex: see Fig. 1). Throughout the range, birds with some white on the head (tendency towards *capistrata* phenotype) are common alongside typical males. Locally, the proportion of such 'aberrant' males reaches 70% (see below for details);

2. Populations showing the diagnostic features of *opistholeuca* (Badakhshan and Hindu Kush). Within the range of these populations a few individuals of the *picata* phenotype occur (not more than 10%). While mixed pairs are evidently a quite common phenomenon (Panov 1989: 87), males showing plumage features intermediate between *opistholeuca* and *picata* are extremely rare;

3. Polymorphic hybridogenous populations '*capistrata* × *opistholeuca*', which presumably now occupy the autochthonous range of the form *capistrata*. They are found in the northeast part of the range of the complex (Figs. 1, 3). Over the whole range of these populations, there is a generally stable ratio of the phenotypes *capistrata* (the overwhelming majority), *opistholeuca*, and birds of the extremely variable phenotype



evreinowi, intermediate between these 2. In the south of the range, in sections contiguous with *picata*, are found small numbers of *picata* males and *picata* × *capistrata* hybrids (total 5.6–11.4%).

In the contact zones of the last group of populations with the 2 others, live hybrid populations whose phenotypic composition is highly variable in space and probably also in time occur. Such populations are known from northeast Afghanistan (Paludan 1959), and from the interfluvium of the Pyandzh and Kyzylsu in Tadzhikistan. In addition, a hybrid population may perhaps exist where the ranges of *opistholeuca* and *picata* meet in northeast Pakistan, and where the form *capistrata* also penetrates via large river valleys from the northwest (Ticehurst 1922, Paludan 1959; see Fig. 1).

Below, we shall examine in more detail: (1) the situation in the range of the polymorphic hybridogenous population *capistrata* × *opistholeuca*; (2) the zone of hybridization found where the range of that population meets the autochthonous *opistholeuca* populations in Tadzhikistan; and (3) the introgression of *capistrata* genes from the polymorphic *capistrata* × *opistholeuca* population into the autochthonous range of *picata* in southern Turkmenistan.

1. Polymorphic hybridogenous populations 'capistrata × opistholeuca'

These populations inhabit low hills in the east of Central Asia and northern Afghanistan—from the relict mountains ('Inselberge') of the Kyzylkum desert in the north to the northern foothills of the Paropamiz and Hindu Kush in the south. Throughout their range (which measures c. 750 m west to east by c. 200 km north to south), they are relatively monotypic in phenotypic composition: among males, the *capistrata* phenotype makes up 68–78% of different samples, and the *opistholeuca* phenotype and *evreinowi*—to all intents and purposes united in a single continuum of variability—from 17.5 to 32%. (The *picata* and *picata* × *capistrata* phenotypes are normally present only in the southernmost parts of the range of these populations—see above and Fig. 3.)

It is quite remarkable that the polymorphism of male plumage coloration is combined with the monomorphic plumage of females: practically all females show the same dull sand-coloured plumage type. Dark (brown-black) females of the *opistholeuca* type are virtually absent from the range of these populations.

Data from the individual marking of birds in the northern range of these groups of populations (Darbaza settlement in southern Kazakhstan, north of Tashkent) indicate the absence of strict mate-selection on

Figure 3. Proportions of different phenotypes (%%) in the autochthonous range of (a) *opistholeuca*, (b), in the range of a polymorphic population 'capistrata × opistholeuca' and (c) in a hybrid population 'capistrata × opistholeuca × opistholeuca' and (d) the range of the form *picata*. Male phenotypes: (e) *opistholeuca*, (f) *evreinowi*, (g) *capistrata*, (h) *capistrata* × *picata*, (i) *picata*. Places where the samples were obtained: 1 = Tadzhik Badakhshan (25 males), 2 = Pyandzh-Kyzylsu interfluvium (62), 3 = Karatau mountains (14), 4 = Babatag mountains (27), 5 = lower reaches of Sherabad river (128), 6 = Nuratau mountains (16), 7 = western foothills of Karzhantau mountains (192), 8 = relict mountains in Kyzylkum desert (Aktau, Tamdytau, Bukantau) (129).

plumage type. As may be seen from the table below, a female having a father of her own phenotype (e.g. *capistrata*) may select as a mate a male of a different phenotype:

Phenotypes of females' fathers	Phenotypes of females' mates		Total number of pairs
	<i>capistrata</i>	<i>opistholeuca</i>	
<i>capistrata</i>	8	2	10
<i>opistholeuca</i>	3	2	5
Total number of pairs	11	4	15

Individual marking also showed that one and the same female may breed with males of different phenotypes in different years.

Support for the hypothesis of genetic polymorphism comes from the inherited plumage characteristics of sons sired by fathers of known phenotypes. As follows from the table below, the progeny of a male of given phenotype may include males of a different phenotype:

Phenotype of fathers	Phenotype of sons			Total number of sons
	<i>capistrata</i>	<i>opistholeuca</i>	<i>evreinowi</i>	
<i>capistrata</i> (12)	14	—	1	15
<i>opistholeuca</i> (4)	2	2	2	6
<i>evreinowi</i> (4)	6	3	2	11
Total number of sons	22	5	5	32

Two of the 4 male *evreinowi* fathers had a plumage type intermediate between *capistrata* and *opistholeuca*; the 2 others were of the *opistholeuca* colour type, with only a slight tendency towards *capistrata*.

It is interesting that males of different phenotypes may be present even within the same brood. In 2 cases we were able to trace the inherited colour pattern through more than one generation. In one such line, the son, his father and grandfather were of the same *opistholeuca* phenotype. In another case, a *capistrata* male having father and grandfather of the same phenotype paired and bred with a female whose father was an *opistholeuca* male. The progeny of this pair included 2 males, one of which was of the *capistrata* phenotype, the other *evreinowi*.

The aforesaid allows the conclusion that the populations considered here represent a genetically homogeneous entity which we suppose to have arisen as a result of penetration by the form *opistholeuca* into the range of *capistrata* and long-term hybridization between them. It may well be that the form *capistrata* no longer exists at the present time as an independent genetic system.

2. Hybrid population found where the polymorphic population '*capistrata* × *opistholeuca*' abuts the range of the autochthonous form *opistholeuca*

In the southeast of western Tadzhikistan, in the interfluvium of the Pyandzh and its tributary the Kyzylsu, studies were made on a transect (of c. 100 km) running from southwest to northeast between the foothills of the Karatau range on the east bank of the Kyzylsu and the eastern slopes of the Khazretishi mountains (Khirmandzhou settlement—see Lyubushchenko & Grabovskiy 1991, and Panov *et al.* in press). Between

the Karatau and Khazretishi ranges lies the South Tadzhik depression with its single, completely isolated mountain Khodzhamumin.

The population of the Karatau foothills is part of the polymorphic population described above: out of 14 males observed, 11 were of the *capistrata* and 3 of the *evreinowi* phenotype. At the opposite, northeast end of the transect (Khirmandzhou), all 18 males recorded were of the *opistholeuca* phenotype. This population occupies the extreme northwest section of the autochthonous *opistholeuca* range.

In the area lying between the points named, on the southern and eastern edge of the South Tadzhik depression and on the slopes of Mt Khodzhamumin, a further 5 demes of 6–24 pairs were studied. The phenotypic composition of such demes is highly variable. Overall, the ratio of *capistrata*, *opistholeuca* and *evreinowi* phenotypes in these 5 demes was 25.8: 48.4: 24.8 ($n=62$), which is significantly different from the composition of all populations from the range of the polymorphic entity '*capistrata* × *opistholeuca*' discussed above (ANOVA; $F=7.22-9.12$, $P<0.00001$).

It is important also that here, unlike in the polymorphic population referred to, female plumage colour varies: alongside the predominant *capistrata* type, *opistholeuca*-type females also occur. We thus have before us a heterogeneous (in the genetic sense) hybrid population in which there has been no stabilization of a monomorphic female phenotype such as is taking place in the hybridogenous polymorphic population '*capistrata* × *opistholeuca*'.

Among the 96 males observed on the transect, 2 were *picata* phenotypes and 3 had plumage intermediate between *picata* and *capistrata*. Two out of 43 females were also of the *picata* plumage type. This small admixture of the *picata* phenotype (5.2% among males) is presumed to be the result of dispersal by individuals of this form from northern parts of the *picata* range lying not far to the south.

3. Migration of *capistrata* genes into the autochthonous range of the form *picata*

We assessed the proportion of *picata*-type males with some white on the head at 4 points on a transect leading along the northwest edge of the *picata* range in southern Turkmenistan. The easternmost point on this transect lies approximately 200–300 km from the contact zone of *picata* and '*capistrata* × *opistholeuca*' populations in north-central Afghanistan (see Paludan 1959). The 3 other samples were collected at points separated from the first and one from another by distances of the same order (Fig. 4). The amount of white in male head plumage was scored on an 8-point scale: 0—pure *picata* phenotype, 7—phenotypically pure *capistrata*.

It is clear from Fig. 4 that males with some white on the head are not uncommon throughout that part of the *picata* range investigated, and in some areas they even outnumber males of the pure phenotype. The cause of this plumage feature in *picata* populations may be: (1) the existence of homologous genes in populations of *picata* and *capistrata*; and (2) introgression of *capistrata* genes into the range of *picata*. In the latter case, the migration of genes may (a) proceed through the generations (owing to

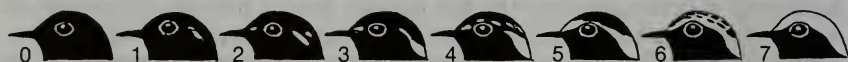
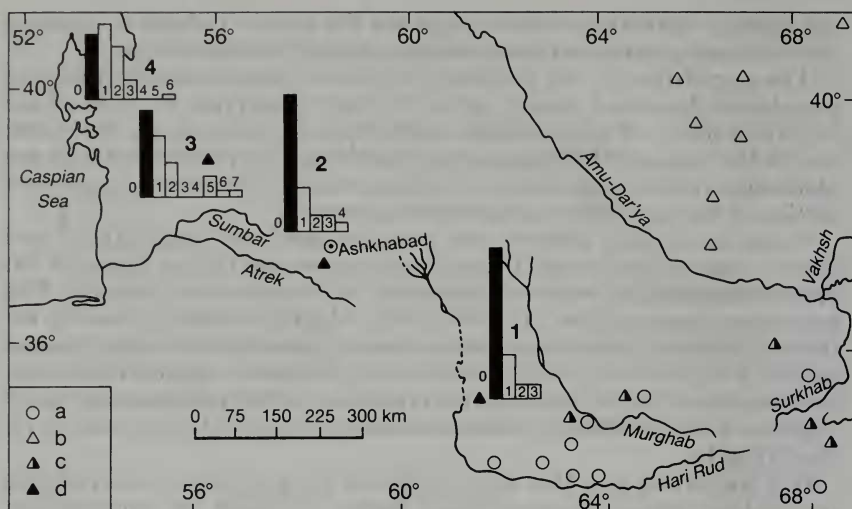


Figure 4. Proportion of males with different head colour (%). Point 1 = Badkhyz ($n=16$); Point 2 = central Kopet-Dag ($n=38$); Point 3 = western Kopet-Dag ($n=33$); and Point 4 = near Krasnovodsk ($n=57$). Head colour scored on point-scale: 0 = pure *picata*; 7 = pure *capistrata*, 1-6 = intermediate ('hybrid') phenotypes. a = records of *picata* on its northern range limit in Afghanistan (from Paludan 1959); b = westernmost records of *capistrata* phenotype males in the USSR; c = records of *capistrata* in northern Afghanistan (Paludan 1959); d = records of breeding *capistrata* in the range of *picata*. In the histograms, the extreme left column (black) shows the proportion in the given sample of typical black-headed *picata* males (score 0). The white columns right of the black column are shown in order of increasing point score (1, 2, 3, and so on).

back-crossing of hybrids, originating in the secondary contact zone of the 2 forms, with representatives of *picata* populations from its autochthonous range), and (b) may result from dispersal by individuals of the form *capistrata* into the range of *picata*.

None of these possibilities can be refuted, but we are inclined to support the hypothesis of gene introgression and, as evidence in favour of supposition 2b, we can at least cite the case of a *capistrata* male paired and breeding successfully with a *picata* female in the central Kopet-Dag (point 3 in Fig. 4; see also Bel'skaya 1961). Furthermore, supposition 2a appears to be contradicted at first sight by an increase in the proportion of 'white-headed' males with increasing distance from the range of *capistrata*.

The latter circumstance may nevertheless be reconciled with the hypothesis of gene migration if one rejects the idea that the flow of alien genes across the range of *picata* is uniform in space and in time. In particular, the dynamics of phenotypic composition may, in principle, be influenced not only by the distance separating a given population from the

source of an alien gene pool, but also by the extent of its separation from other birds of genetically the same stock. In this regard, it is significant that the plumage feature of partial 'white-headedness' has its widest distribution in the western Kopet-Dag and in the low hills of the south-east Caspian region, where suitable *picata* nesting habitat is patchily distributed rather than uniformly as in the central Kopet-Dag. In semi-isolated demes inhabiting widely separated mountain ranges, new plumage features can become fixed comparatively quickly, such features in the present case having been introduced into the given deme by alien *capistrata* genes (for further details, see Panov *et al.* in press).

Discussion

According to the proposed scenario, the 'Eastern Pied Wheatear' complex is a standard polytypic species comprising 3 geographical races, all of which were originally monomorphic in respect of male plumage colour. These races separated off and diverged in conditions of geographical isolation and then, as a result of range expansion, entered into secondary contact and hybridization.

It was precisely the mixing of the gene pools of the 3 originally autonomous population groups which determined that phenotypic dissimilarity in Eastern Pied Wheatears which is generally called 'polymorphism'. In our view, this concept is, in its generally accepted sense (see e.g. Mayr & Stresemann 1950), not applicable to the case under investigation. In fact, what we have before us is either 'pseudopolymorphism' (see Panov 1989), i.e. the simultaneous existence of representatives of 2 or 3 *different taxa* in the area of their secondary contact (as is the case, for example, in the Pyandzh-Kyzylsu interfluve), or 'hybridogenous polymorphism' which has arisen as a result of long-term introgressive hybridization (of the population '*capistrata* × *opistholeuca*').

Taking this scenario as a whole, it may be assumed that the first stage in its development was the simultaneous separation of a single ancestral species into 3 population groups. One of these (the present-day *picata*) separated off in the Iranian highlands; the second (*opistholeuca*) in the western mountain regions of Central Asia; the third (*capistrata*) originally inhabited the lower parts of the western Gissaro-Alay mountains and adjoining areas.

The latter scheme cannot completely accommodate a number of facts which (if they have been correctly interpreted) may indicate that the forms in question have attained different levels of divergence and, therefore, may differ one from another genealogically (i.e. in evolutionary age). One gains the impression that *picata* and *opistholeuca* are most probably sister taxa, while *capistrata* stands somewhat apart. This supposition gains strength from the fact that *picata* and *opistholeuca* on the one hand and *capistrata* on the other differ with respect to the type of sexual dimorphism, particular features of communication behaviour, and preferred habitats.

After consideration of the foregoing, one may imagine 2 ways in which the *Oenanthe picata* complex may have emerged. The first option envisages a single ancestral form originally splitting into 2 population groups which

may provisionally be called 'low-mountain' and 'high-mountain'. The first group eventually produced the form *capistrata*, the second split in the course of time into the forms *picata* and *opistholeuca*.

The second option supposes the complex to have emerged through 2 successive invasions into its present range from the range of ancestral taxa generally believed to be African, Middle Eastern and southwest Asian wheatears of the superspecies *lugens*—*lugentoides*—*lugubris* (see e.g. Panov 1989, Tye 1989). Moreover, the immigrants in one case may have come from the range of *lugens*, males of which have the same type of plumage pattern as *capistrata* males and comparatively large measurements. Another wave of colonists may have originated from the range of the *lugubris* group, males of which characteristically have a high degree of pigmentation, which is also a typical feature of the forms *picata* and *opistholeuca* (Tye 1989: 173).

In order to discover which of the proposed scenarios is closest to the truth, there is a need for further comparative investigations within the 'Eastern Pied Wheatear' complex, and also for a comparison of the various representatives of this group with the still little-known wheatears of the *lugens*—*lugentoides*—*lugubris* complex. It is recommended that priority in such future studies be given to approaches which focus on comparative ethology and molecular genetics.

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